

What drives ponderosa pine regeneration following wildfire in the western United States?



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ABSTRACT

Ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson) is a prominent tree species in forests of the western United States. Wildfire activity in ponderosa pine dominated or co-dominated forests has increased dramatically in recent decades, with these recent wildfires often burning in an uncharacteristic manner due to past land management activities and changing climate. The structure and function of vegetative communities that develop following recent wildfires are highly contingent on ponderosa pine regeneration, making it important that the factors influencing this regeneration be thoroughly understood. In this evidence-based review, we qualitatively synthesized publications that examined how the post-fire abundance of ponderosa pine regeneration was related to such factors. We identified 33 relevant publications, from which we synthesized relationships for 21 factors. Numerous publications indicated that distance to seed source (e.g., distance to nearest live overstory tree or group of trees) was a factor that clearly affected post-fire ponderosa pine regeneration abundance; with few exceptions, these publications demonstrated that as distance to seed source increased, the amount of regeneration decreased. Climatic stress (e.g., Palmer Drought Severity Index, actual evapotranspiration, climatic moisture deficit) and elevation also emerged as well-studied factors with a clear relationship to post-fire regeneration abundance. Specifically, areas with lower climatic stress and/or at higher elevations generally harbored more regeneration than areas with higher climatic stress and/or at lower elevations; together, these factors highlight that cooler, moister environments enhance regeneration. The other 18 factors were either well studied but did not have consistent relationships with regeneration abundance, or were not well studied, highlighting research areas that could benefit from further attention. Overall, the strong influence of distance to seed source, climatic stress, and elevation on post-fire ponderosa pine regeneration abundance has important implications for post-fire vegetative recovery and management, particularly in light of recent and predicted changes in wildfire activity and climate.

1. Introduction

Ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson) is a widely distributed tree species in the western United States (US) (Oliver and Ryker, 1990). Wildfires have long been a keystone natural disturbance for forests dominated or co-dominated by ponderosa pine (hereafter collectively referred to as ponderosa pine forests). While the fire regimes of ponderosa pine forests varied across space and time prior to Euro-American settlement in the mid- to late-18th century, they were largely dominated by frequent low- to moderate-severity surface fires (Swetnam and Baisan, 1996; Brown and Cook, 2006; Scholl and Taylor, 2010) or by mixed-severity fires that included some component of high-severity crown fire (Arno et al., 1995; Iniguez et al., 2009; Sherriff

et al., 2014). These historical fires promoted a heterogeneous condition comprised of generally small non-forested areas mixed with generally open forest stands (Fulé et al., 1997; Churchill et al., 2017; Battaglia et al., 2018). Importantly, when climatic conditions were not exceedingly warm and dry, these historical fires also enhanced opportunities for ponderosa pine to regenerate (Arno et al., 1995; Kaufmann et al., 2000; Taylor, 2010).

Several life history characteristics of ponderosa pine promoted its regeneration under historical fire regimes. Ponderosa pine is a non-sprouting, non-serotinous conifer, and its relatively large seeds do not generally disperse long distances or remain viable for long periods in the soil seed bank (Howard, 2003); thus, its regeneration following wildfire is highly reliant on seeds produced by nearby surviving trees.

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While small trees were often killed by historical wildfires, large, mature trees commonly survived due to their thick bark, thick bud scales, open crown, deep rooting habit, and other fire adaptations, and therefore provided an available seed source (Howard, 2003). Ponderosa pine seeds germinate best on bare soil (Howard, 2003), which historical wildfires exposed by consuming litter, duff, and other surface fuels. Ponderosa pine is fairly shade-intolerant, and the survival and growth of ponderosa pine germinants was favored by the relatively open forest conditions created under historical fire regimes (Oliver and Ryker, 1990; Howard, 2003).

Wildfires in western US ponderosa pine forests are no longer burning as they did historically. Fire suppression, logging, grazing, and other activities since Euro-American settlement excluded wildfire activity in most ponderosa pine forests for much of the 20th century (Arno et al., 1995; Fulé et al., 1997; Iniguez et al., 2009), causing forests to become increasingly dense and homogeneous and allowing surface fuels to accumulate (Brown and Cook, 2006; Scholl and Taylor, 2010; Battaglia et al., 2018). In more recent decades, however, there has been a resurgence of wildfire activity across much of the range of ponderosa pine (Miller and Safford, 2012; Dennison et al., 2014; Singleton et al., 2019). The amount and extent of high-severity burning has also increased, with recent wildfires sometimes containing treeless or nearly treeless high-severity patches 100 s or even 1000 s of hectares in size (Miller and Safford, 2012; Stevens et al., 2017; Singleton et al., 2019). The increase in wildfire activity and severity has been credited to the changes in forest structure and surface fuels caused by fire exclusion, as well as to a warming and drying climate (Westerling et al., 2006; Fulé et al., 2012; Harris and Taylor, 2015). And while some recently burned areas contain abundant regeneration (Savage et al., 2013; Malone et al., 2018), in other areas regeneration is sparse (Dodson and Root, 2013; Ouzts et al., 2015; Davis et al., 2019), generating concern about forest resilience (*sensu* Holling, 1973).

Because the structure and function of the vegetative communities that develop following wildfires are highly contingent on post-fire tree regeneration, it is important that the factors driving tree regeneration be thoroughly understood. Critically, identifying which factors govern ponderosa pine regeneration abundance can help land managers efficiently plan appropriate post-fire management activities. For example, the National Forest Management Act of 1976 requires that US Forest Service managers promptly and adequately reforest timber-producing stands that have been “denuded or deforested” by wildfire or other disturbances such as logging; if managers can anticipate where post-fire regeneration will be insufficient to meet this requirement, then they can better plan efforts like tree planting. Similarly, knowing which areas might experience excessive post-fire regeneration can allow managers to better plan efforts such as prescribed fire to reduce the amount of regeneration.

A growing number of publications have examined relationships between the abundance of ponderosa pine regeneration following recent wildfires and a wide variety of potentially influential factors. These publications demonstrate that multiple factors appear to be at play, including those related to climate (Rother and Veblen, 2017; Davis et al., 2019; Hankin et al., 2019), topography (Dodson and Root, 2013; Rother and Veblen, 2016; Haffey et al., 2018), understory vegetation (Bonnet et al., 2005; Ziegler et al., 2017; Downing et al., 2019), and the wildfires themselves (Chambers et al., 2016; Haire and McGarigal, 2010; Rodman et al., 2019). To date, however, there has not been an effort to synthesize these publications for the scientific and land management communities. We conducted an evidence-based review to identify which factors that potentially influence ponderosa pine regeneration abundance have been examined, and to qualitatively synthesize the evidence pertaining to each. We then placed the results of our review in the context of the broader literature, identified research gaps, and made post-fire management recommendations. While other researchers have conducted similar reviews of post-fire tree regeneration in western US forests, they integrated findings for multiple species

(North et al., 2019; Stevens-Rumann and Morgan, 2019). Yet, these species may have unique relationships with the studied factors due to variations in their life history characteristics. By focusing our review on ponderosa pine specifically, we hope to provide valuable information that will help sustain this prominent species in the face of fire regime and climatic changes.

2. Methods

Evidence-based reviews have been increasingly conducted by forestry researchers to synthesize the literature on particular topics (e.g., Peppin et al., 2010; Hicke et al., 2012; Kalies and Yocom-Kent, 2016). Such reviews aim to minimize bias by using objective, rigorous, and transparent methods (Pullin and Stewart, 2006; Lortie, 2014; Haddaway et al., 2015). To address our topic of interest, we conducted an evidence-based review that adopted the following steps: (1) using defined search strings and multiple databases to identify potentially relevant publications, including grey publications; (2) screening potentially relevant publications using defined inclusion criteria; (3) extracting and critically appraising the evidence from relevant publications using defined procedures; and (4) qualitatively synthesizing the evidence according to defined procedures. Each of these steps is described in more detail below.

We began our review by conducting online literature searches using the search string ((ponderosa pine OR *Pinus ponderosa*) AND (fire OR burn) AND (seedling OR regeneration OR recruitment)). We conducted searches in July–September 2018 using the databases Web of Science, Google Scholar, and JSTOR, as well as the library databases of western US universities accredited by the Society of American Foresters. We supplemented the publications produced by the initial search with additional publications that we deemed missing based on our personal knowledge of the subject; in most cases, the missing publications had simply been published after we conducted our literature searches.

We screened the above potentially relevant publications in two stages. First, we cursorily screened publications to eliminate those that clearly did not meet all of our inclusion criteria (Table 1). Then, we carefully screened the remaining publications to determine if all criteria were met. If we were unable to assess from the text whether a potentially relevant publication met all criteria, we sought clarification from the corresponding author. This process helped us ensure that our review was as inclusive and as accurate as possible. Most of the clarification we sought at this stage was regarding studies that did not analyze post-fire ponderosa pine regeneration *per se* as the response variable, but instead analyzed regeneration for a multi-species group (e.g., all conifers, all pines); for these studies, we inquired whether this multi-species regeneration was strongly dominated by ponderosa pine (i.e., ponderosa pine comprised > 75% of regenerating trees).

We extracted a variety of information from the relevant publications into a spreadsheet. Information extracted included: (1) publication citation and type; (2) geographic state(s); (3) number of wildfire(s) examined; (4) time since wildfire(s); (5) regeneration response variable(s) examined; (6) explanatory variable(s) examined; and (7) relationship(s) between regeneration variable(s) and explanatory variable(s). We assessed the relationships, or evidence, as either positive, negative, neutral, or variable. We made these assessments using the reported results of formal statistical tests (e.g., p-values), if available; if unavailable (e.g., correlations were reported but p-values were not), we made relationship assessments based on descriptions of the results in the text. As needed, we sought clarification from the corresponding author about extracted information. We critically appraised the evidence by evaluating its quality. High-quality evidence came from refereed journal articles that incorporated data from multiple fires, while lesser-quality evidence came from either refereed journal articles that utilized data from only one fire, or from other publication types.

To conduct our qualitative synthesis, we first arranged closely related explanatory variables into groups that we called factors (e.g., fine

Table 1

Inclusion criteria for publications utilized in our review of the factors driving ponderosa pine regeneration abundance following wildfire.

Criteria category	Criteria description
Population	<ul style="list-style-type: none"> Publication analyzed naturally-regenerated ponderosa pine trees in recent wildfires <ul style="list-style-type: none"> If a publication analyzed post-fire regenerating ponderosa pine trees as part of a multi-species group (e.g., all conifers), it was included if ponderosa pine was by far the dominant species in the group (i.e., ponderosa pine comprised 75% or more of regenerating trees in the group) If a publication analyzed post-fire regenerating ponderosa pine trees that were a mix of artificially- and naturally-regenerated individuals, it was included if most (i.e., 75% or more of regenerating trees) were naturally-regenerated
Intervention	<ul style="list-style-type: none"> Publication analyzed any continuous (e.g., elevation) or categorical (e.g., fire severity categories) explanatory variable of post-fire regeneration
Comparator	<ul style="list-style-type: none"> Publication analyzed lower values of the intervention relative to higher values (continuous or categorical interventions; e.g., lower relative to higher elevations), or no intervention relative to alternative interventions (categorical interventions; e.g., overstory was not thinned relative to thinned prior to wildfire)
Outcomes	<ul style="list-style-type: none"> Publication analyzed any continuous (e.g., regeneration density) or categorical (e.g., regeneration absence or presence) measure of post-fire regeneration abundance as the response variable
Other	<ul style="list-style-type: none"> Publication was a refereed journal article, government report, conference proceedings article, thesis, or dissertation Publication presented primary, empirical research Publication was not duplicative (e.g., a thesis that was later published as a refereed journal article)

surface fuel abundance, which includes variables like litter cover, litter depth, and fine wood cover), and then arranged factors into overarching categories (e.g., substrates, which includes fine surface fuel abundance as well as coarse surface fuel abundance, bare soil abundance, and rock abundance). In all, 21 factors emerged, which were distributed across eight categories. These 21 factors exclude those that were poorly replicated (i.e., they were examined in only one or two studies), because they were not well-suited to synthesis. We avoided simply vote-counting when synthesizing (Lortie, 2014); rather, we considered both the number of publications and the quality of the evidence within them when we determined whether a particular factor appeared to have an overall positive, negative, neutral, or variable relationship to post-fire regeneration abundance.

3. Results

We found 33 publications that met our inclusion criteria (Appendix A), out of 58 publications that we considered to be potentially relevant. Of the 33 publications, 30 are refereed journal articles, one is a conference proceedings article, and two are theses. All publications were produced between 1996 and 2019, and half were produced between 2016 and 2019, underscoring the highly emergent nature of this area of research. The authors conducted research for these publications in > 100 wildfires distributed across eight states (Fig. 1), with a greater number of publications examining wildfires in Arizona (13 publications), Colorado (9 publications), New Mexico (9 publications), and South Dakota (6 publications) than in other states.

3.1. Distance to seed source

We identified 17 publications that examined some metric of distance to seed source and post-fire ponderosa pine regeneration abundance (Table 2; Figs. 2 and 3). Distance to seed source was measured across these studies in a variety of ways, including distance to the nearest individual live overstory ponderosa pine tree (e.g., Malone et al., 2018), distance to the nearest ten live overstory ponderosa pine trees (e.g., Kemp et al., 2016), and distance to the nearest live forest edge (e.g., Chambers et al., 2016).

We found that 14 of the 17 studies identified distance to seed source as being negatively correlated with regeneration abundance (Bonnet et al., 2005; Chambers et al., 2016; Coop et al., 2019; Davis et al., 2019; Downing et al., 2019; Haffey et al., 2018; Haire and McGarigal, 2010; Kemp et al., 2016; Malone et al., 2018; Owen et al., 2017; Rodman et al., 2019; Rother and Veblen, 2016; Stevens et al., 2014; Ziegler et al., 2017). Of those who found negative relationships between ponderosa pine regeneration and distance, threshold distances appeared to vary somewhat. Working in 21 northern Rockies wildfires, Kemp et al. (2016) found that the probability of encountering regeneration was low

at distances > 60 m. Similarly, Bonnet et al. (2005) showed that distances of 0–50 m supported relatively high densities of tree regeneration in the Jasper Fire of South Dakota, with limited regeneration present at longer distances. However, for ten wildfires in the southwestern US, 150–200 m was identified as a threshold beyond which few seedlings were observed (Haire and McGarigal, 2010; Haffey et al., 2018). While Owen et al. (2017) demonstrated that this negative relationship to distance generally held true, they also showed that plot size was important for observing the low density of seedlings within the interior of high-severity burned patches (> 200 m from a living tree) for two wildfires in Arizona. Similarly, Malone et al. (2018) found that there was generally a negative relationship, but also found that the distribution of regeneration followed the distribution of available space, suggesting that seed sources were not limiting for the relatively short distances they sampled (< 50 m). The other three studies found no relationship between distance and regeneration (Wutke, 2011; Kemp et al., 2019; Porter, 2019). Wutke (2011) found no relationship between regeneration and distance to a live tree on the Jasper Fire, South Dakota, though regeneration was only measured at distances of 50 m and 150 m. Similarly, Porter (2019) found no relationship to distance to live trees, but this study had relatively low occurrences of ponderosa pine seedlings across all plots (35% of plots contained at least one seedling) and short distances were relatively undersampled (12% of plots were at distances of < 50 m). Kemp et al.'s (2019) work on multiple fires in the northern Rockies showed no correlation between ponderosa pine regeneration and distance to a live tree when climate relationships were accounted for, even though distance was correlated with Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) regeneration.

3.2. Fire severity

Seventeen studies examined how fire severity affected ponderosa pine regeneration abundance (Table 2; Fig. 3). While fire severity and distance to seed source have some relationship (i.e., high-severity areas are generally further from seed sources than lower-severity areas), given the vast differences in how severity was measured across studies and the inherent differences in scale of these two factors, we felt it necessary to assess them separately. Across studies, severity was measured in multiple ways including Monitoring Trends in Burn Severity (MTBS) derived burn severity categories (e.g., Kemp et al., 2016), percent crown damage (e.g., Bonnet et al., 2005), percent overstory density mortality (e.g., Stevens-Rumann et al., 2012), percent overstory basal area mortality (e.g., Rodman et al., 2019), or a combination of methods (e.g., Kemp et al., 2019). Additionally, multiple studies used the same metric of severity, percent overstory density mortality for example, to create severity categories, but the severity categories were defined differently. For example, Stevens-Rumann et al. (2012) binned severity into 20% overstory mortality categories, with 80–100%

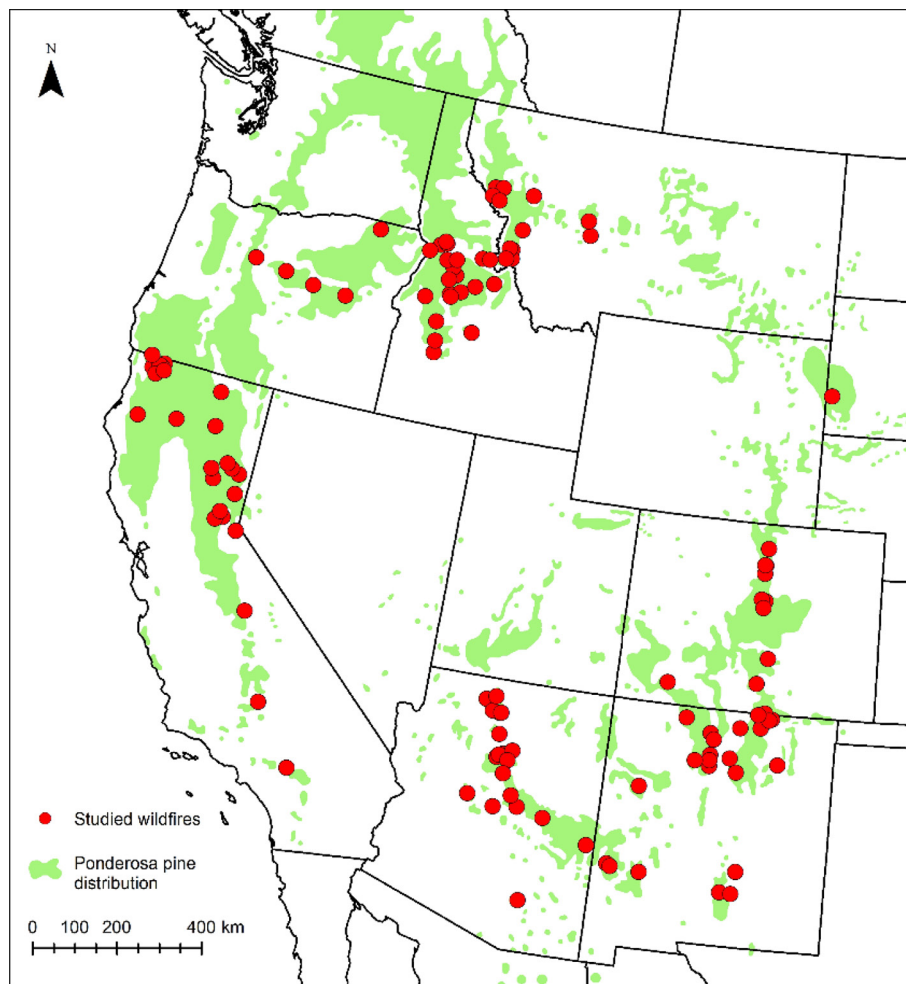


Fig. 1. Map of the approximate distribution of ponderosa pine in the western United States (Little 1971), as well as the approximate locations of wildfires studied in the 33 publications that we incorporated in our review.

mortality the highest severity category, while [Lentile et al. \(2005\)](#) identified 100% mortality as the highest severity category.

The effects of fire severity were highly variable across the 17 studies. Eight found some evidence of a negative relationship between regeneration and severity, meaning increases in severity resulted in decreases in regeneration ([Chambers et al., 2016](#); [Davis et al., 2019](#); [Haire and McGarigal, 2010](#); [Keyser et al., 2008](#); [Lentile et al., 2005](#); [Roccaforte et al., 2018](#); [Stevens-Rumann et al., 2012](#); [Wutke, 2011](#)). For example, [Roccaforte et al. \(2018\)](#) found tree regeneration declined as overstory tree mortality increased in the Southwest and [Davis et al. \(2019\)](#) found declines in regeneration with increases in satellite-derived burn severity in the northern Rockies. One of these eight studies, [Stevens-Rumann et al. \(2012\)](#), found one of the study fires, the Pumpkin Fire in Arizona, did not have a significant relationship between regeneration and severity, while regeneration did decline significantly with increasing severity following the Jasper Fire in South Dakota. On the other hand, four studies found some evidence of a positive relationship with severity ([Bonnet et al., 2005](#); [Malone et al., 2018](#); [Rodman et al., 2019](#); [Shive et al., 2013](#)). For these studies, high-severity areas could sometimes contain or be adjacent to surviving overstory trees. For example, [Bonnet et al. \(2005\)](#) found that regeneration increased as the cover of overstory trees with > 50% crown consumption increased, meaning live trees were potentially present at the highest levels of severity. Finally, five studies found that fire severity did not have a meaningful relationship to ponderosa pine regeneration ([Kemp et al., 2016](#); [Rother and Veblen, 2016](#); [Stoddard et al., 2018](#); [Downing et al., 2019](#); [Kemp et al., 2019](#)). This null

relationship may also be due to the classification of severity. For example, in [Stoddard et al. \(2018\)](#) and [Rother and Veblen \(2016\)](#), high-severity classified sites may have included some proportion of living trees. Conversely, in [Downing et al. \(2019\)](#), a range of satellite-derived burn severity values was examined, but all plots were located in areas of 100% overstory mortality.

3.3. Pre-fire overstory conditions

Nine publications reported relationships between pre-fire overstory condition explanatory variables and post-fire ponderosa pine regeneration abundance ([Table 2](#)). We divided the variables into two factors. The first factor incorporates variables that categorically indicate whether or not stands experienced overstory thinning treatments prior to wildfire. Thinning treatments in ponderosa pine forests are widely implemented to reduce the potential for uncharacteristic high-severity fire ([Stephens et al., 2009](#); [Safford et al., 2012](#); [Lydersen et al., 2017](#)), and thus this factor can reflect fire severity. The second factor incorporates variables that are continuous measures of pre-fire overstory structure. This factor can serve as an indicator of potential fire severity, with denser stands generally having greater potential for high-severity fire, or as an indicator of site productivity, with denser stands being generally more productive.

Four publications contrasted post-fire ponderosa pine regeneration abundance between stands that had been thinned prior to wildfire and stands that had not been thinned ([Table 2](#); [Fig. 4](#)). While results were technically mixed, as a whole they suggested that thinned stands

Table 2
The 33 publications that we incorporated into our review, and a summary of their relationships between explanatory factors and ponderosa pine regeneration following wildfire. The relationships between factors and regeneration are indicated by symbols: + (positive), – (negative), 0 (neutral), and × (variable). We assigned multiple relationships (e.g., 0/–) for a factor when a publication examined multiple explanatory variables and the variables yielded different results (e.g., Bonnet et al., 2005), or when a publication treated study sites as case studies and the sites yielded different results (e.g., Stevens-Rumann et al., 2012).

Publication	Factor category					Understory vegetation	Substrates
	Distance to seed source	Fire severity	Pre-fire overstory conditions	Time since fire	Topography		
Bonnet et al. (2005)	(–)	(+)			Aspect (0); Slope (0)	Moisture (0); Temperature (0)	Bare soil abundance (0/–); Rock abundance (0); Fine fuel abundance (+/0/–); Coarse fuel abundance (0)
Chambers et al. (2016)	(–)	(–)	Pre-fire overstory structure (0)		Elevation (+); Aspect (0); Slope (0); Topographic Wetness Index (0); Heat Load Index (0)	Moisture (0)	Total understory abundance (0)
Coop et al. (2019)	(–)			(+)		Moisture (+); Climatic stress (–)	
Davis et al. (2019)	(–)	(–)					
Dodson and Root (2013)			Pre-fire overstory structure (0)	(+)	Elevation (+); Heat Load Index (0)		Total understory abundance (0)
Downing et al. (2019)	(–)	(0)	Pre-fire overstory structure (0)	(0)	Elevation (x)	Climatic stress (+/0/x)	Woody understory abundance (+)
Foxx (1996)				(+)			
Haffey et al. (2018)	(–)				Elevation (+); Aspect (–); Topographic position (+)		
Haire and McGaigal (2010)	(–)	(–)		(+)	Elevation (+); Topographic position (0); Topographic Wetness Index (+/0); Heat Load Index (0)	Herbaceous understory abundance (0); Woody understory abundance (0/–)	Bare soil abundance (0); Rock abundance (0/–)
Hankin et al. (2019)				(+)		Moisture (0); Temperature (0/–); Climatic stress (–)	
Kemp et al. (2016)	(–)	(0)	Pre-fire overstory structure (0)	(0)	Elevation (0); Heat Load Index (0)	Total understory abundance (0)	
Kemp et al. (2019)	(0)	(0)					
Keyser et al. (2008)		(–)					
Lentile et al. (2005)		(–)					
Lopez Ortiz et al. (2019)					Elevation (+); Aspect (+)		
Malone et al. (2018)	(–)	(+)			Elevation (x); Topographic Wetness Index (x)	Woody understory abundance (+/x)	Fine fuel abundance (+)
Ouzts et al. (2015)							
Owen et al. (2017)	(–)					Woody understory abundance (+/0)	
Passovoy and Fulé (2006)				(0)			
Porter (2019)	(0)				Elevation (0); Aspect (0); Slope (0)		
Roccaforte et al. (2012)				(0)			
Roccaforte et al. (2018)		(–)	Pre-fire overstory thinning treatments (0)				Fine fuel abundance (0); Coarse fuel abundance (0)
Rodman et al. (2019)	(–)	(+/0/x)	Pre-fire overstory structure (+)	(+)	Topographic position (0)	Herbaceous understory abundance (0/–); Woody understory abundance (+/0/–)	Bare soil abundance (0); Rock abundance (0); Fine fuel abundance (0)
Rother and Veblen (2016)	(–)	(0)			Elevation (+); Aspect (+); Slope (0)	Herbaceous understory abundance (0); Woody understory abundance (0)	Bare soil abundance (0); Rock abundance (0); Fine fuel abundance (0); Coarse fuel abundance (0)

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Table 2 (continued)

Publication	Factor category		Time since fire	Topography	Climate	Understory vegetation	Substrates
	Distance to seed source	Fire severity	Pre-fire overstory conditions				
Rother and Veblen (2017)				(+)	Moisture (+); Temperature (0); Climatic stress (-)		
Savage et al. (2013) Shive et al. (2013)		(+)	Pre-fire overstory thinning treatments (+)				
Stevens et al. (2014)	(-)		Pre-fire overstory thinning treatments (+)				
Stevens-Rumann et al. (2012)		(0/-)					
Stoddard et al. (2018) Strom and Fulé (2007)		(0)	Pre-fire overstory thinning treatments (0)	(0)			
Wutke (2011) Ziegler et al. (2017)	(0) (-)	(-)		(+)	Aspect (-); Slope (-); Topographic position (0)	Woody understory abundance (+)	

contained more post-fire regeneration than unthinned stands because thinned stands were less apt to burn severely (Strom and Fulé, 2007; Shive et al., 2013; Stevens et al., 2014; Roccaforte et al., 2018). For example, Stevens et al. (2014) compared regeneration densities in thinned versus unthinned stands distributed across 12 California wildfires, and found that thinned stands had greater regeneration densities. Likewise, Strom and Fulé (2007), Shive et al. (2013), and Roccaforte et al. (2018) each focused on a single Arizona wildfire, and found that regeneration densities were three to four times greater in thinned than unthinned stands post-fire; however, statistical differences in densities were difficult to detect due to a high degree of variability within the thinned and unthinned classes.

Five publications examined the relationship between pre-fire overstory structure (e.g., basal area, density) and the abundance of post-fire ponderosa pine regeneration abundance (Table 2). For these publications, pre-fire overstory structure was probably indicative of site productivity since three exclusively worked in areas of high severity (Dodson and Root, 2013; Chambers et al., 2016; Downing et al., 2019) and the other two stated such (Kemp et al., 2016; Rodman et al., 2019). Regardless, four publications, which together utilized data collected in 31 wildfires in four states, found the relationship to be non-significant (Dodson and Root, 2013; Chambers et al., 2016; Kemp et al., 2016; Downing et al., 2019). In contrast, one publication, which utilized data from 15 wildfires in two states, found a positive relationship (Rodman et al., 2019).

3.4. Time since fire

Thirteen publications examined the relationship between time since fire and post-fire ponderosa pine regeneration abundance (Table 2). The authors of these publications utilized one of three approaches for examining this relationship. The first, a chronosequence approach, substitutes space for time by sampling wildfires of various ages (e.g., Passovoy and Fulé, 2006). The second, a repeated measures approach, samples the same sites at multiple times since fire (e.g., Foxx, 1996). These two approaches provide information on the total abundance of regenerating trees at a given sampling time. Finally, a tree aging approach uses dendrochronology (e.g., Rother and Veblen, 2017) or whorl counting (e.g., Haire and McGarigal, 2010) to determine in what years trees established following wildfire.

All 13 publications found either a positive time since fire relationship with regeneration abundance, or no relationship. Positive relationships were documented in nine of these publications (Davis et al., 2019; Dodson and Root, 2013; Downing et al., 2019; Foxx, 1996; Haire and McGarigal, 2010; Hankin et al., 2019; Rodman et al., 2019; Rother and Veblen, 2017; Wutke, 2011). For example, a repeated measures study conducted for 16 years following New Mexico's La Mesa Fire found that regeneration increased through time (Foxx, 1996). Similarly, a tree aging study conducted in 33 wildfires also showed that regenerating trees generally continued to establish through time, causing total regeneration to increase, although it also showed that establishment rates generally slowed through time due to increasingly harsh climatic conditions (Davis et al., 2019). Meanwhile, four publications found no relationship to time since fire (Passovoy and Fulé, 2006; Roccaforte et al., 2012; Kemp et al., 2016; Stoddard et al., 2018). Two of these studies, which used a chronosequence approach, attributed the absence of a trend to highly variable patterns of regeneration across fires (Passovoy and Fulé, 2006; Roccaforte et al., 2012). In one repeated measures study conducted in the Leroux Fire, Arizona, a time since fire trend could not be detected because regeneration was negligible throughout the 15-year post-fire observation period (Stoddard et al., 2018).

3.5. Climate

Researchers investigated the relationship between climatic variables



Fig. 2. We found strong evidence that distance to seed source affects post-fire ponderosa pine regeneration abundance, with regeneration decreasing with increasing distance. This photo illustrates this phenomenon in the Jasper Fire, South Dakota, 14 years following burning. Photo credit: Paula J. Fornwalt.

and post-fire ponderosa pine regeneration in eight publications (Table 2). We divided climatic variables into three factors: moisture, temperature, and climatic stress. Climate has a strong influence on the distribution of plant species, and explorations of plant-climate relationships (e.g., bioclimatic envelopes (Law et al., 2019)) can help ecologists predict conditions that support species occurrence. Moreover, successful regeneration requires not only germination but

survival, and climatic conditions at all stages of development are important to consider when determining factors that influence regeneration.

Moisture, which includes variables characterizing precipitation and soil moisture, was examined for relationships with post-fire ponderosa pine regeneration in six publications (Table 2). There were no conclusive trends, with two of the publications showing a positive effect of

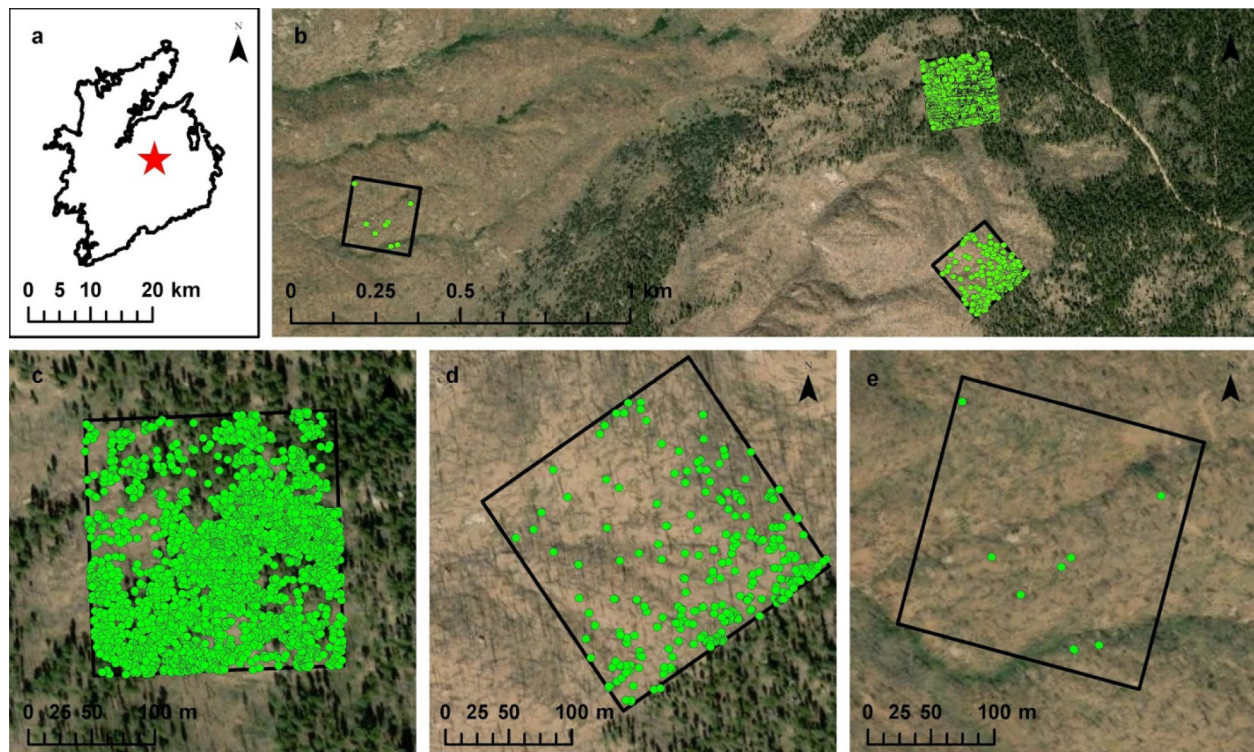


Fig. 3. Post-fire ponderosa pine regeneration (green points) varied with respect to fire severity and distance to seed source for three 4-ha study plots (Ziegler et al., 2017; Malone et al., 2018) at a study site in the Hayman Fire, Colorado (a, b). (c) One plot was located in an area that burned primarily with low to moderate severity, and had abundant regeneration. (d) One plot burned with high severity, but was near surviving trees; it had a modest amount of regeneration, much of which was located within ~100 m of survivors. (e) The final plot also burned with high severity, but was > 200 m from surviving trees; it had sparse regeneration. Imagery credit: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, and/or CNES/Airbus. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



Fig. 4. The results of our review indicate that stands subjected to overstory thinning treatments prior to wildfire tended to have greater post-fire ponderosa pine regeneration than those that were not. This pair of photos, taken in study plots (Stevens et al., 2014) five years after the Peterson Fire, California, illustrates this result. (a) This plot was thinned prior to the fire and contained some regeneration. (b) This plot was not thinned prior to the fire and did not contain any regeneration. Photo credit: Jens T. Stevens.

moisture (Rother and Veblen, 2017; Davis et al., 2019) and the other four showing no effect (Bonnet et al., 2005; Chambers et al., 2016; Hankin et al., 2019; Kemp et al., 2019). Rother and Veblen (2017) studied five wildfires in Colorado and found that pulses of post-fire establishment largely occurred in years with above-average growing season precipitation. In addition, the authors found that years of establishment pulses tended to have at least one growing season month with precipitation that exceeded the 90th percentile. Davis et al. (2019) investigated 33 wildfires across the western US, finding a positive relationship between establishment pulse years and average soil moisture of the driest month of the year. In contrast, Hankin et al. (2019) found that pulses of establishment did not correlate with growing season precipitation anomalies one to three years before, during, or one to three years after the year of the pulse for 18 wildfires in the northern Rockies. Similarly, Bonnet et al. (2005), who examined mean summer soil moisture two years post-fire, Chambers et al. (2016), who examined 30-year mean annual precipitation, and Kemp et al. (2019), who looked at 30-year mean spring and summer precipitation and summer soil moisture, failed to find that these moisture variables had a meaningful relationship with regeneration density.

Four publications examined the relationship between temperature and post-fire ponderosa pine regeneration (Table 2; Fig. 5). Temperature includes variables characterizing air temperature and soil temperature. Two of these publications found relationships between temperature and post-fire ponderosa pine regeneration abundance (Hankin et al., 2019; Kemp et al., 2019). Hankin et al. (2019) determined that growing degree days and maximum air temperature during the growing season were significantly lower than the 30-year average during and two years prior to ponderosa pine establishment pulses, although minimum and average air temperature during the growing season were not (Fig. 5). Kemp et al. (2019) determined that mean summer temperature was the only factor that influenced regeneration density, with densities highest at intermediate values (14.8 °C). In contrast, two publications covering seven states found minimal evidence of a relationship between regeneration and mean summer soil temperature (Bonnet et al., 2005) and mean growing season air temperature (Rother and Veblen, 2017).

Seven publications reported on relationships between climatic stress explanatory variables and post-fire ponderosa pine regeneration abundance (Table 2; Fig. 5). Climatic stress variables all strongly reflect both moisture and temperature, and include length of drought, actual evapotranspiration (AET), Palmer Drought Severity Index (PDSI), vapor pressure deficit (VPD), climatic moisture deficit (CMD), and climatic

water deficit (CWD). The length of drought is the time period associated with both drier and warmer than average conditions (Stahle et al., 2009). AET is the amount of water removed from the surface due to evaporation and plant transpiration if total water amount is not limited (Pidwirny, 2006). PDSI integrates temperature and precipitation to create a dryness index, with lower values being drier than higher values (Palmer, 1965). VPD is the difference between the amount of moisture in the air and how much moisture it can hold at saturation (Will et al., 2013). CMD is the difference between reference evapotranspiration and precipitation (Hargreaves and Samani, 1985; Wang et al., 2016), while CWD is the difference between potential and actual evapotranspiration (Stephenson, 1998).

There was relatively strong agreement across the seven climatic stress publications, with five generally finding a negative relationship between climatic stress and post-fire ponderosa pine regeneration, one finding mixed results (Downing et al., 2019), and one finding no relationship (Kemp et al., 2019). Savage et al. (2013) identified the length of drought that occurs prior, during, and after establishment to be significant in predicting regeneration density and illustrated a negative relationship between AET and post-fire regeneration based on studying five fires in New Mexico. Similarly, Rother and Veblen (2017) found that years of strong post-fire ponderosa pine establishment pulses had greater mean growing season PDSI values (~ 5) than other years (~ 1) for five Colorado wildfires, indicating that pulses tended to occur in years with less stressful growing seasons. Likewise, Davis et al. (2019) showed that establishment pulses became more apt to occur as mean summer VPD in the year of establishment became increasingly lower than the long-term average. Moreover, Hankin et al. (2019) found that establishment pulses had establishment-year growing season mean CMDs that were significantly lower than the 30-year average, but they also found that three years prior to establishment pulses, growing season mean CMDs were significantly greater than average, which they speculated may have initiated cone production (Fig. 5). Finally, Rodman et al. (2019) illustrated that low 30-year average CWD and high 30-year average AET were related to higher regeneration densities. For example, CWD values of 0 mm had regeneration densities of ~ 400 stems/ha while values over 200 mm had densities of ~ 0 stems/ha (Rodman et al., 2019). Rodman et al. (2019) also found that 30-year averages for CWD and AET were better predictors of regeneration density than 3-year post-fire averages. In contrast, Downing et al. (2019) found that average annual CMD during the post-fire period was an inconsistent predictor of post-fire ponderosa pine regeneration density for four fires in Oregon; they also found that annual CMD was

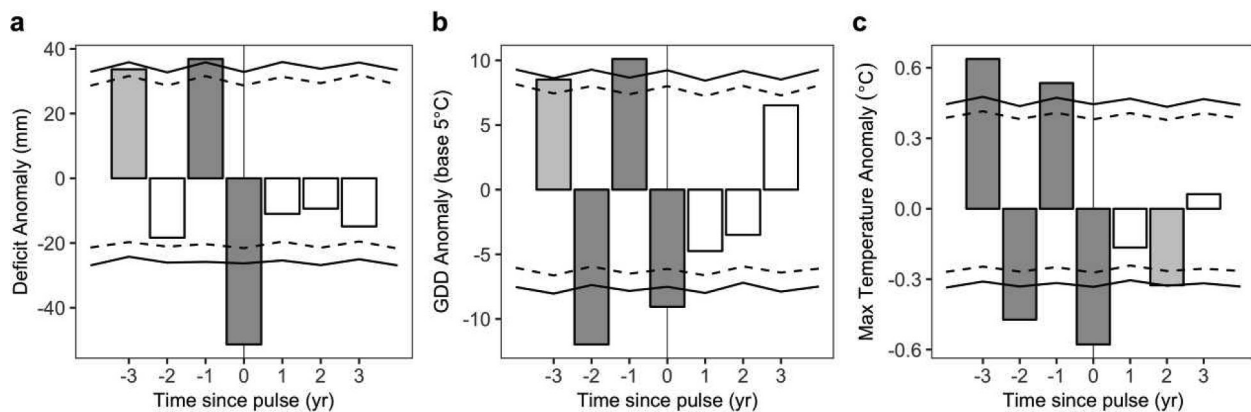


Fig. 5. We identified climatic stress as a major factor that limited ponderosa pine regeneration following wildfire. This figure, adapted from [Hankin et al. \(2019\)](#), summarizes Superposed Epoch Analysis (SEA) results that present mean climate anomalies for a climatic stress explanatory variable ((a) climatic moisture deficit) as well as two temperature explanatory variables ((b) growing degree days (GDD), (c) maximum temperature) before, during and after 44 ponderosa pine regeneration events from 33 sites in Idaho and Montana. Climate was detrended using a 30-year running mean and annual values were subtracted from the mean over the time period to obtain anomaly values. Growing degree days were determined from a base of 5 °C. 90% and 95% confidence intervals were based on 10,000 simulations under the null hypothesis.

not correlated with annual establishment. The authors hypothesized that their lack of clear findings may be because CMD was too spatially coarse and/or too temporally homogeneous to detect meaningful relationships ([Downing et al. \(2019\)](#)).

3.6. Topography

Thirteen papers investigated the relationship between topographic explanatory variables and post-fire ponderosa pine tree regeneration abundance ([Table 2](#)). These variables were divided into six factors: elevation, aspect, slope, topographic position, Topographic Wetness Index (TWI), and Heat Load Index (HLI). While many of these topographic factors can be viewed as climate proxies (e.g., elevation and aspect, with low elevations and southern aspects generally having warmer/drier climates than high elevations and northern aspects), we examined topographic factors independent of climate factors to maintain as much alignment with the source papers as possible.

Researchers quantified elevation in ten studies, with overall strong agreement among them ([Table 2](#)). Six of these studies, which were collectively conducted in 33 fires, illustrated a positive relationship between elevation and pine regeneration ([Haire and McGarigal, 2010; Dodson and Root, 2013; Chambers et al., 2016; Rother and Veblen, 2016; Haffey et al., 2018; Lopez Ortiz et al., 2019](#)). [Dodson and Root \(2013\)](#) found significant regeneration above 1400 m in Oregon's Eyerly Fire ten years post-fire, and minimal regeneration below 1030 m. In Colorado, [Chambers et al. \(2016\)](#) determined that post-fire ponderosa pine regeneration densities more than doubled every 200 m between 2200 and 2600 m for high-severity portions of five wildfires; regeneration densities were estimated to be 21, 51, and 124 stems/ha at 2200, 2400, and 2600 m, respectively. Similarly, [Rother and Veblen \(2016\)](#) found that regeneration was scant in six Colorado wildfires below 2368 m. [Haffey et al. \(2018\)](#) and [Lopez Ortiz et al. \(2019\)](#) found more regeneration at higher elevations in eight New Mexico and Arizona wildfires and in 11 California and Oregon wildfires, respectively. In contrast, two publications found that elevation had a variable relationship with regeneration ([Malone et al., 2018; Downing et al., 2019](#)). [Downing et al. \(2019\)](#), for example, found a non-linear relationship between elevation and regeneration for four fires in Oregon, with ponderosa pine regeneration being most abundant at intermediate elevations. Finally, two publications showed no relationship between elevation and regeneration abundance ([Kemp et al., 2016; Porter, 2019](#)).

Researchers investigated aspect as a potential factor driving post-fire ponderosa pine regeneration abundance in seven papers ([Table 2](#)).

There was no clear trend between aspect and regeneration. Two papers, collectively conducted in 11 fires in California and six fires in Colorado, indicated that there was a positive relationship between northerly aspects and post-fire ponderosa pine regeneration ([Rother and Veblen, 2016; Lopez Ortiz et al., 2019](#)). In contrast, two papers found a negative relationship between northeasterly aspects and post-fire ponderosa pine regeneration ([Ziegler et al., 2017; Haffey et al., 2018](#)). [Haffey et al. \(2018\)](#) suggested that, for their eight wildfires in Arizona and New Mexico, ponderosa pine regeneration on more northeasterly aspects may have been limited by greater competition from post-fire understory vegetation. Finally, no correlation between aspect and regeneration was found in three studies that collectively examined six fires across South Dakota and Colorado ([Bonnet et al., 2005; Chambers et al., 2016; Porter, 2019](#)).

Slope, examined in five publications, was a topographic variable that did not generally have a meaningful overall relationship with regeneration abundance ([Table 2](#)). [Ziegler et al. \(2017\)](#) found that slope affected regeneration abundance for three fires in Colorado and South Dakota, with greater regeneration on shallow than steep slopes. Yet, [Bonnet et al. \(2005\)](#) showed no correlation between slope and regeneration in one South Dakota fire, and [Chambers et al. \(2016\), Rother and Veblen \(2016\), and Porter \(2019\)](#) found no relationship between slope and regeneration in six collective fires in Colorado.

Five papers presented information on the relationship between topographic position and post-fire ponderosa pine regeneration abundance ([Table 2](#)). Topographic position is scale-dependent and refers to whether a particular location is in the lower, middle, or upper part of the defined landscape ([Guisan et al., 1999](#)). Four of these publications found no clear relationship ([Haire and McGarigal, 2010; Ziegler et al., 2017; Malone et al., 2018; Porter, 2019](#)). In contrast, [Haffey et al. \(2018\)](#) found higher regeneration in upper rather than lower topographic positions, but did not consider it a strong factor because it had low importance in their model.

Researchers calculated two topographic indices to quantify microclimate-related topographic variables: TWI and HLI ([Table 2](#)). Three publications collectively found no clear trend for TWI, which is an index of water availability that incorporates both slope and the upslope area that drains into it ([Beven and Kirby, 1979](#)). [Chambers et al. \(2016\)](#) and [Malone et al. \(2018\)](#) found no relationship and a variable relationship, respectively, between TWI and post-fire ponderosa pine regeneration, while [Haire and McGarigal \(2010\)](#) found a strong positive relationship between TWI and regeneration for one fire in New Mexico and no relationship for another fire in Arizona. Five studies calculated HLI, a solar exposure index that incorporates slope, aspect and latitude

(McCune, 2007); all found no relationship between HLI and post-fire ponderosa pine regeneration (Haire and McGarigal, 2010; Dodson and Root, 2013; Chambers et al., 2016; Kemp et al., 2016; Downing et al., 2019).

3.7. Understory vegetation

Eleven publications examined how post-fire ponderosa pine regeneration was related to various post-fire understory vegetation explanatory variables (Table 2). Relationships between regeneration and understory vegetation variables are commonly explored to gain insight into whether regeneration is being driven by competitive (negative relationships) or facilitative (positive relationships) processes; however, it is important to recognize that they do not prove that these processes are occurring. We grouped these variables to create three factors: total understory vegetation abundance, herbaceous understory vegetation abundance, and woody understory vegetation abundance.

Four publications analyzed relationships between total post-fire understory vegetation abundance variables (e.g., total understory richness, total understory cover) and ponderosa pine regeneration abundance (Table 2). Three of these publications, which examined total understory cover collectively across 27 wildfires in four states, found the relationship to be non-significant (Dodson and Root, 2013; Chambers et al., 2016; Kemp et al., 2016). In contrast, one publication, which examined both total understory richness and total understory cover in a South Dakota wildfire, found a negative relationship (Bonnet et al., 2005).

Researchers investigated the correlation between herbaceous understory vegetation abundance (e.g., graminoid cover, forb cover) and post-fire ponderosa pine regeneration abundance in three publications (Table 2). Results were mixed. One publication examined 15 wildfires in Colorado and New Mexico and reported that graminoid cover was negatively related to regeneration density while forb cover was unrelated (Rodman et al., 2019); the other two collectively examined eight wildfires in Arizona, Colorado, and New Mexico and reported that neither graminoid or forb cover were related to regeneration (Haire and McGarigal, 2010; Rother and Veblen, 2016).

Seven publications reported on how the abundance of woody understory vegetation, such as shrubs and other regenerating trees, was related to ponderosa pine regeneration following wildfire (Table 2). A clear trend was not apparent. Two publications indicated that increased woody plant abundance had a positive relationship with regeneration (Ziegler et al., 2017; Downing et al., 2019), one indicated that the relationship was neutral (Rother and Veblen, 2016), and four indicated that the relationship was either positive, neutral, negative, or variable, depending on the specific woody plant variable or wildfire analyzed (Haire and McGarigal, 2010; Malone et al., 2018; Owen et al., 2017; Rodman et al., 2019). For example, Downing et al. (2019) found that in severely burned portions of four Oregon wildfires, as shrub cover increased, so did ponderosa pine regeneration density; indeed, shrubs overtopped 26% of the regenerating pines, and some of these pines were beginning to emerge from the shrub canopy. Ziegler et al. (2017) utilized 4-ha stem maps of post-fire tree regeneration in severely-burned portions of one South Dakota and two Colorado wildfires, and showed that at fine scales (e.g., < 10 m), regenerating ponderosa pine locations were positively associated with the locations of other regenerating trees (i.e., they were spatially aggregated), regardless of tree species. Owen et al. (2017) similarly utilized 4-ha stem maps in severely-burned portions of two Arizona wildfires, finding that at fine scales, the locations of regenerating ponderosa pine trees were positively associated with the locations of other regenerating ponderosa pine trees but were independent of the locations of regenerating sprouting trees such as Gambel oak (*Quercus gambelii* Nutt.). Meanwhile, Rodman et al., 2019 found that for 15 wildfires in Colorado and New Mexico, ponderosa pine regeneration density decreased with increasing Gambel oak regeneration, increased with increasing Douglas-

fir regeneration density, and showed no change with increasing shrub cover.

3.8. Substrates

We identified seven publications that reported how post-fire ponderosa pine regeneration was related to substrate explanatory variables (Table 2). Many of these substrate variables may directly affect regeneration (e.g., fine surface fuels like litter can obstruct bare soil, which is considered ideal for germination), or they may indirectly affect regeneration by influencing growing conditions (e.g., fine surface fuels like litter can moderate soil temperature and moisture). We parsed these variables into four factors: bare soil abundance, rock abundance, fine fuel abundance, and coarse fuel abundance.

Four publications examined relationships between bare soil abundance (specifically, bare soil cover) and post-fire ponderosa pine regeneration (Table 2). These publications provided little evidence of a relationship (Bonnet et al., 2005; Haire and McGarigal, 2010; Rodman et al., 2019; Rother and Veblen, 2016). Bonnet et al. (2005) reported that regeneration in the Jasper Fire was not strongly associated with unburned bare soil cover, although it was negatively associated with burned bare soil cover. Haire and McGarigal (2010), Rother and Veblen (2016), and Rodman et al., 2019 reported that regeneration was not strongly associated with bare soil cover (burn status not specified) for 23 wildfires collectively studied in the Southwest.

Relationships between rock abundance and post-fire ponderosa pine regeneration abundance were looked at in four publications (Table 2). Three of these, for which research was collectively done in 22 wildfires, indicated that rock cover did not meaningfully relate to regeneration (Bonnet et al., 2005; Rodman et al., 2019; Rother and Veblen, 2016). The fourth publication showed that rock cover did not have a meaningful relationship with regeneration in one wildfire and that it had a negative relationship in another (Haire and McGarigal, 2010).

Six publications investigated how various explanatory variables describing fine fuel abundance, such as litter cover, duff cover, and small-diameter wood load, related to ponderosa pine regeneration following wildfire (Table 2). The publications did not point to a clear relationship. Specifically, Ouzts et al. (2015) found a positive association between litter cover and regeneration in high-severity patches of eight wildfires in Arizona and New Mexico. Similarly, Bonnet et al. (2005) found in the Jasper Fire that regeneration was also positively associated with litter cover, so long as cover was derived from freshly cast scorched needles and was covering burned soil. Bonnet et al. (2005) further found that regeneration was not strongly related to blackened or partially consumed pre-fire litter cover, and was negatively related to unburned pre-fire litter cover. Four other studies, by Roccaforte et al. (2012), Chambers et al. (2016), Rother and Veblen (2016), and Rodman et al. (2019), did not find strong relationships between various fine fuels variables and regeneration; these studies were collectively conducted in ten Colorado, 11 Arizona, and 11 New Mexico wildfires.

Finally, five publications examined the relationship between coarse fuel (e.g., large-diameter wood) abundance and post-fire ponderosa pine regeneration (Table 2; Fig. 6). These studies were collectively conducted across 33 wildfires in three states. None of the studies found that coarse fuel abundance conferred a meaningful effect on regeneration (Bonnet et al., 2005; Chambers et al., 2016; Roccaforte et al., 2012; Rodman et al., 2019; Rother and Veblen, 2016).

4. Discussion

Ponderosa pine forests of the western US have witnessed a dramatic increase in wildfire occurrence, size, and severity in recent decades (Westerling et al., 2006; Stevens et al., 2017; Singleton et al., 2019), and a body of literature characterizing the ecological consequences of these wildfires is emerging. Our synthesis is the first to focus strictly on

ponderosa pine regeneration and provides insight on how 21 factors shape its post-fire abundance (Fig. 7). Of the numerous publications that examined distance to seed source, most showed that it had a strong, negative relationship with post-fire ponderosa pine regeneration abundance. Climatic stress and elevation also emerged as well-studied factors that had relatively clear relationships with post-fire regeneration abundance; areas having lower climatic stress and/or at higher elevations generally harbored more regeneration than those having higher climatic stress and/or at lower elevations. Relationships between regeneration and the other factors were less clear, either because they did not have consistent trends or because they were not as well studied.

4.1. Wildfire patterns influence regeneration

The spatial complexity of how a wildfire burns across a landscape greatly impacts its subsequent recovery. Throughout the literature covered in this review, distance to seed source was one of the most well-studied and consistent factors driving post-fire regeneration. Many studies demonstrated that seed rain from living ponderosa pine trees is limited on the low end to 37 m (Boldt et al., 1983), or approximately 1–1.5 times adjacent tree heights (Shepperd and Battaglia, 2002), to 75–100 m (Barrett, 1966) or 200–400 m from live seed trees (Haire and McGarigal, 2010; Kemp et al., 2016). Distances beyond 90–200 m from a living tree saw little to no ponderosa pine regeneration. Critical distances to a living seed source vary substantially by tree species, especially with variations in wind versus animal dispersed species (e.g., Coop and Schoettle, 2009; Leirfallom et al., 2015), as well as serotinous versus non-serotinous species (e.g., Kemp et al., 2016). Thus understanding distance dynamics by species is important for improving management recommendations in different ecosystems. However, many studies in more mixed conifer systems that include a ponderosa pine component were excluded from this analysis because relationships between individual species and potential factors were not examined (e.g., Stevens-Rumann and Morgan, 2016).

Many of the wildfire-related factors, such as distance to seed source, severity, and pre-fire treatments, appear to be interacting with one another or other factors identified in this literature review, which makes separating out any patterns difficult. For example, one of the most frequently researched factors in our literature review was fire severity, but patterns were variable with a majority of papers illustrating negative and neutral effects on post-fire regeneration and fewer papers showing positive or variable effects (Fig. 7). Severity has often served as a proxy for distance to seed source; however, there is a lack of congruence in the classification of severity and the scale at which these processes function. To quantify the relationship between severity and distance to seed source, two factors are critical. First is the classification of high severity: 100% overstory tree mortality or below 100%. If the latter, than seed sources may be close to areas sampled for tree regeneration. Second, if high severity is identified as 100% mortality, the patch size of that high-severity area becomes important for determining the seed source relationship. For instance, the difference in distance to seed source is substantial between a 100-m² patch with 100% tree mortality and a 1000-m² patch. This question is rarely assessed in conjunction with either severity or distance to seed source at a plot level, although there have been some recent exceptions (e.g., Downing et al., 2019). While many authors hypothesize that high-severity fires will generally have low post-fire ponderosa pine regeneration, it is important to note that regeneration is highly variable due to confounding factors such as distance to seed source, elevation, and other post-fire factors (e.g., see Fig. 3d).

Similarly, it has been demonstrated repeatedly in ponderosa pine and other dry forest types, stands subjected to recent thinning treatments are less apt to burn with high severity than those with no treatments (Stephens et al., 2009; Safford et al., 2012; Lydersen et al., 2017). Thus, in the four studies that examined pre-fire thinning, treated stands tended to have greater amounts of post-fire regeneration than

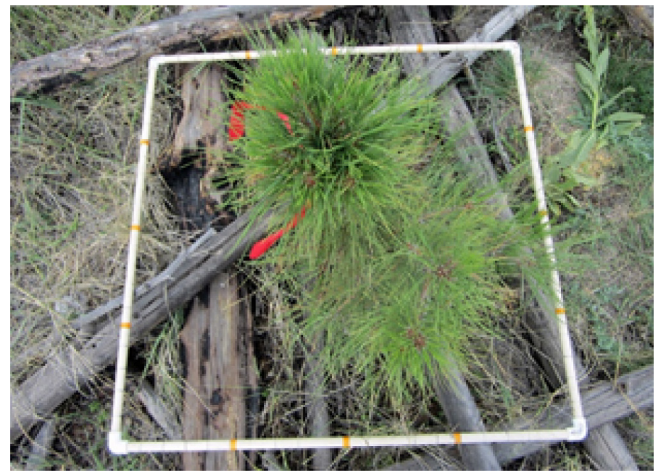


Fig. 6. This photo, taken 13 years after the Pumpkin Fire, Arizona, shows a regenerating ponderosa pine tree in a localized area with abundant coarse wood. However, none of the publications we identified found that coarse wood abundance had an effect, either positive or negative, on regeneration abundance. Photo credit: Suzanne M. Owen.

untreated. This finding is also tightly linked to differences in distance to seed source and fire severity.

Throughout much of the reviewed literature, wildfires were visited at one point in time to assess reforestation that is inevitability changing year by year and occurring on much longer time scales. Several studies assessed tree seedling establishment through time using varying methods, but most studies were still relatively short post-fire periods (< 20 years), especially when considering the lifespan of ponderosa pine. Better integration of dendrochronology techniques and projecting conditions of these sites into the future will enable us to understand how areas once dominated by ponderosa pine recover to similar forest types or perhaps convert to non-forest types following large fires, especially in light of a changing climate.

4.2. Climatic and topographic influences on regeneration

Researchers examined a wide range of climatic and topographic variables as potential factors influencing post-fire ponderosa pine regeneration across the western US. Climate has a strong influence on vegetation and thus understanding how bioclimatic envelopes influence vegetation development following disturbance is important (Law et al., 2019). Numerous regional studies have illustrated that the distribution of ponderosa pine across western North America can be predicted through a combination of precipitation and temperature variables (Gray and Hamann, 2013; Rehfeldt et al., 2014). Ponderosa pine regeneration requirements include specifically timed moisture events during establishment periods as evident by historical age structure with age cohorts associated with optimal climate and periodic regeneration failures associated with historical warm-dry periods (Savage et al., 1996; Fulé et al., 1997; Savage et al., 2013). Water availability following high-severity fire is crucial for ponderosa pine seedlings to survive high surface temperatures after organic and vegetation layers have been removed (Kolb and Robberecht, 1996).

We did not identify either moisture or temperature per se as strong factors associated with regeneration; however, we did identify some patterns that justify further research to assist in identifying bioclimatic envelopes for ponderosa pine following wildfire given that climate change is and will continue to increase wildfire frequency and extent (Law et al., 2019). Our review highlighted growing season precipitation and soil moisture of the driest month during the germination period as potential moisture variables that may have a strong influence on post-fire ponderosa pine regeneration (Rother and Veblen, 2017; Davis et al.,

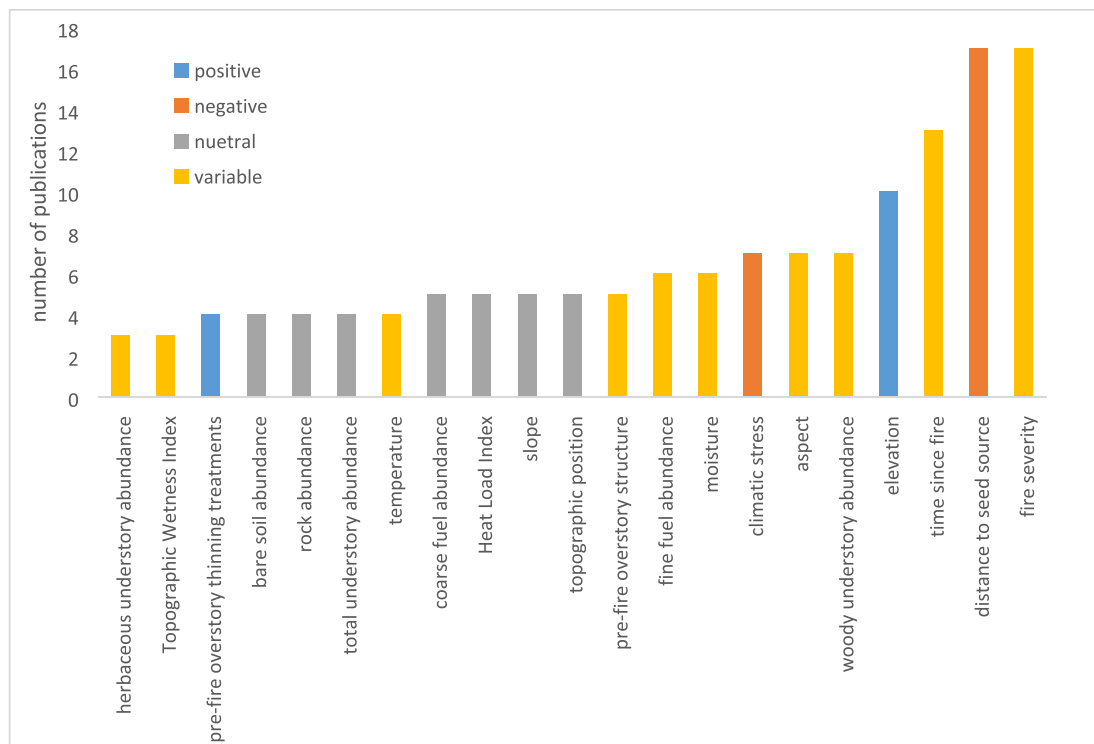


Fig. 7. Number of publications that examined each of the 21 factors in our review of post-fire ponderosa pine regeneration abundance, and the overall relationship between each factor. We based our classification decision on both the number of publications demonstrating each relationship as well as the quality of the evidence in the publications.

2019). Likewise, temperature variables were also inconclusive and require more-detailed studies. Growing degree days, maximum growing season and mean summer air temperature in the germination year all appear to influence post-fire ponderosa pine regeneration but no clear trends across multiple studies emerged in our review (Hankin et al., 2019; Kemp et al., 2019).

However, we did find that climatic stress, which integrates moisture and temperature, is a strong factor influencing post-fire ponderosa pine regeneration abundance. Regeneration in ponderosa pine historically has been episodic and linked to periods of cooler, fire-free periods (Brown and Wu, 2005; Meunier et al., 2014). Even over shorter time periods, studies have found ponderosa pine regeneration strongly linked to the cool and moist climatic conditions (e.g., Hankin et al., 2019; Rodman et al., 2019; Rother and Veblen, 2017). However, in some cases, especially in the southwestern US, episodic regeneration may occur so infrequently, that even the longest studies presented in our review may not capture regeneration potential, with the last region-wide pulse of ponderosa pine regeneration establishment dating back to ~1919 (Savage et al., 1996). In other regions, however, more frequent regeneration pulses or conducive climatic conditions should capture regeneration patterns in these shorter time periods (Davis et al., 2019). In all regions, it is likely that under the right combination of conditions (e.g., low climatic stress, higher elevations, close proximity to seed source), future ponderosa pine seedlings will establish and thrive post-fire even under a warmer and drier climate. Thus, judgements on the lack of observed regeneration should be made with caution given long recovery periods may be more prevalent in a more unfavorable climate.

Given future projections of a warmer and drier climate, it is critical to understand post-fire ponderosa pine regeneration sensitivity to climatic stress in order to minimize forest to non-forest type conversion (Law et al., 2019). Specifically, our review highlighted that ponderosa pine regeneration pulses are moisture limited and that climatic stress variables such as summer VPD and CWD have increased over the past few decades and recently crossed threshold values making future

climate conditions less favorable for ponderosa pine regeneration pulses (Davis et al., 2019; Hankin et al., 2019; Rodman et al., 2019; Rother and Veblen, 2017). In addition, ponderosa pine has been shown to be more sensitive and thus vulnerable under different projected climate change scenarios than other tree species (Rehfeldt et al., 2014; Kemp et al., 2019). Kemp et al. (2019) predicted that under the worst case climate projections (RCP 8.5), 82% of their study sites would have temperatures $\geq 17^{\circ}\text{C}$, which would result in low post-fire ponderosa pine regeneration and therefore high susceptibility to type conversion without active forest management and only 10% of these sites would have productive, natural post-fire regeneration. One solution to supporting ponderosa pine regeneration even with less favorable climate conditions in the future is to identify topoclimatic “refugia” that is conducive to tree establishment even when landscapes on the whole are less suitable to natural regeneration conditions (Keppel et al., 2015; McCullough et al., 2017).

Finally, topographic variables such as elevation and aspect are easy to measure and therefore can be logical climate proxies. There is a well-known inverse relationship between climate and elevation in the western US: as elevation increases, temperature decreases and precipitation increases, thus lowering evaporative demand and alleviating climatic stress (Larson et al., 2008; Dodson and Root, 2013). We found that elevation was a strong factor for predicting post-fire ponderosa pine regeneration, with higher elevations having greater regeneration abundance than lower elevations. In contrast, other topographic factors were not good predictors for post-fire regeneration. For example, aspect was a factor that was adequately researched, but there was no clear trend; some papers showed higher regeneration on northerly aspects, others on southerly aspects, and some highlighted that aspect had no impact due to other factors having a greater influence on post-fire regeneration. Specifically, on some southerly aspects, post-fire ponderosa pine regeneration was aided by understory vegetation that most likely served as nurse plants, and in contrast on some northerly aspects, vegetation acted as a competitor for limited resources (Ziegler et al.,

2017; Haffey et al., 2018). Designing research studies to account for interacting factors would help tease apart the role aspect plays in post-fire ponderosa pine regeneration.

4.3. Regeneration responses to understory vegetation and substrates

We found that understory vegetation did not relate to post-fire ponderosa pine regeneration in a consistent manner: evidence of positive (and thus potentially facilitative), neutral, and negative (and thus potentially competitive) interactions were uncovered across the three factors. This variability may be due, at least in part, to the differences in understory composition that existed across the study sites the publications collectively utilized. For example, some sites contain woody understory species that can regenerate rapidly and extensively following wildfire, which can compete with ponderosa pine regeneration (Rodman et al., 2019); other sites contain woody understory species that regenerate more slowly and patchily, and have little effect on regeneration (Rother and Veblen, 2016). It may also be partly due to differences in the study sites' climatic conditions, with positive relationships potentially more apt to occur at more harsh sites (e.g., higher climatic stress) and negative relationships potentially more apt to occur at less harsh sites (e.g., lower climatic stress) (Bertness and Callaway, 1994). We encourage researchers to continue to examine the relationship between understory vegetation and ponderosa pine regeneration in burned environments, and how this relationship is shaped by site factors, so that a deeper understanding can be gained.

Substrate factors were poorly studied relative to other factor categories, and the limited available evidence suggests that they may not have a major influence on the abundance of post-fire ponderosa pine regeneration. Of the four substrate factors we synthesized, fine fuels (e.g., litter, duff, small-diameter wood) appeared to be most apt to affect regeneration, with two of the six publications indicating that fine fuel abundance and regeneration abundance were positively related. Any beneficial effect of fine fuels may be due to their ability to ameliorate harsh climatic conditions (Bonnet et al., 2005), such as those encountered in high-severity burn areas. Coarse surface fuels can also improve climatic conditions, and have been shown to benefit post-fire tree regeneration following wildfire in other forest types (Coop and Schoettle, 2009; Castro et al., 2011). Indeed, US Forest Service tree planting guidelines for western National Forests (e.g., Region 3 Supplement 2409.17-2002-1) recommend that managers plant trees near coarse surface fuels or other "shade" objects to capture this benefit, particularly on climatically stressful sites. Yet surprisingly, none of the five publications we reviewed showed a positive relationship between coarse fuels and ponderosa pine regeneration. Additional observational and experimental research into how fine fuels, coarse fuels, and other substrates affect regeneration in ponderosa pine forests could help improve our currently limited understanding.

4.4. Other research recommendations

In addition to the research recommendations mentioned above, we suggest that research in two additional areas be conducted. First, a meta-analysis that quantitatively examines how one or more of the factors we qualitatively synthesized affect post-fire ponderosa pine regeneration, would enhance our understanding of the strength or dominance of these factors across the range of ponderosa pine. Second, the use of modeling to explore how post-fire ponderosa pine regeneration may be affected by climate change would have scientific and management implications for ponderosa pine systems.

As a meta-analysis, we propose the use of statistical analyses of raw data or results from multiple independent studies. The use of statistics on a large, range-wide data set would better inform how various factors affect post-fire ponderosa pine regeneration and could provide additional clarity on factors that showed conflicting results across studies. Several meta-analyses have in fact been done (e.g. Shatford et al., 2007;

Stevens-Rumann et al., 2018; Davis et al., 2019), but the literature is currently lacking range wide analyses. Additionally, a species specific dataset could identify important breakpoints such as a critical distance from a seed source or climatic conditions beyond which no ponderosa pine regeneration occurred. Further, we found that researchers were not consistent in definitions of commonly used factors, like fire severity, but this could be corrected in a meta-analysis.

The influence of climate on post-fire regeneration is a growing research field as demonstrated by the multiple studies that examined climate factors in just the last few years. Several of these studies have already detected regeneration failures due to climate change, particularly in areas where climatic stress is already high, such as at lower elevations (Feddema et al., 2013; Davis et al. 2019). Understanding how climate change may continue to affect regeneration in the future is critical for identifying where long-lasting post-fire type conversions are likely to occur and for determining where management can mitigate these effects. In the future, as bioclimatic envelopes contract and/or shift due to climate change (Kemp et al., 2019), it will be important to understand how climate is limiting seed production, germination, and seedling establishment. In some locations, climate change may alter fire severity, fire frequency or fire size, leaving many areas without regeneration even when climate is favorable for regeneration processes. For example, repeated, high-severity fires in ponderosa pine forests are already promoting the transition to non-forested ecosystems in southwestern US forests (Coop et al., 2016; Walker et al., 2018). In other locations, germination and establishment may be limited by an unfavorable future climate (Davis et al., 2018, 2019). Quantifying the role of both future climatic limitations on seedlings as well as the impact of changing fire regimes are critical for identifying potential management strategies in current and future burned landscapes.

4.5. Management recommendations

There is broad consensus that post-fire forest management activities should emphasize restoring ecosystem function and promoting resilience to future conditions (Lynch et al., 2000; Binkley et al., 2008; North et al., 2009; Larson and Churchill, 2012; Churchill et al., 2013). Ecological recovery of ponderosa pine in high-severity patches historically had temporal and spatial variation as a fundamental component of post-fire forest development (Shatford et al., 2007). Similarly, ecological recovery today will have temporal delays in natural regeneration and variation in regeneration densities across the landscape due to abiotic and biotic regeneration factors. However, unlike historical post-fire recovery, warmer, drier climates will add new challenges to recovery from high-severity fires such as shifting climatic envelopes for ponderosa pine germination and establishment (Davis et al., 2019; Kemp et al., 2019). In addition to climate changes, changes in fire regimes, especially in the frequency of high-severity burns (or repeated fires) may challenge the ability of seedlings to establish even when climate and site conditions are conducive to regeneration (e.g. Coop et al., 2016, Stevens-Rumann and Morgan, 2016, Falk et al., 2019). This possibility and increasing probability of reburning in the future should play an important role in determining how and where to conduct post-fire forest management (Stevens-Rumann and Morgan, 2019).

Results from our review can help land managers better predict post-fire ponderosa pine regeneration outcomes and in turn prioritize post-fire management investments. Our review indicated that post-fire ponderosa pine regeneration is likely to be highest in areas near surviving trees and therefore tree planting or other artificial regeneration approaches in these areas are probably not needed (North et al., 2019). Such areas include forest that burned with low to moderate severity (i.e., non-stand-replacing fire), as well as forest that burned with high severity (i.e., stand-replacing fire) but is adjacent to areas of lesser severity. Over time, naturally regenerating trees in these areas may not need to be actively managed, or they may need to be thinned with mechanical and/or prescribed fire treatments to prevent the

development of dense, homogenous forests that decrease ecosystem resilience. Conversely, our review indicated that post-fire ponderosa pine regeneration is likely to be lowest in areas far from surviving trees; indeed, several of the publications we reviewed indicated that these areas were in fact nearly devoid of regeneration (e.g., [Chambers et al., 2016](#); [Haffey et al., 2018](#)). Planting trees may be a viable management strategy for these areas.

Our review also revealed that factors such as elevation and climatic stress are important predictors of regeneration, and these factors may help further refine where active management may be needed. For instance, because higher elevations within the range of ponderosa pine tended to support greater levels of post-fire regeneration than lower elevations (e.g., [Haffey et al., 2018](#); [Kemp et al., 2019](#); [Lopez Ortiz et al., 2019](#)), higher elevations may confer the best chance of survival for planted trees in areas far from a seed source. Similarly, our literature review highlighted that areas with lower climatic stress had higher post-fire regeneration than higher climatic stress areas (e.g., [Savage et al., 2013](#); [Rother and Veblen, 2017](#); [Davis et al., 2019](#)), inferring that planting trees in lower climatic stress areas would enhance survivorship.

[Donato et al. \(2009\)](#) recommended creating post-fire distance to seed source maps as a tool to identify planting needs. Based on our literature review, we recommend that prior to mapping seed sources and dispersal distances, managers must first identify present and future bioclimatic envelopes for ponderosa pine forests given that many of these forests have already crossed climatic thresholds where the climate

is no longer suitable for ponderosa pine regeneration ([Davis et al., 2019](#); [Kemp et al., 2019](#)). Managers can then use seed sources, seed dispersal distances and other important post-fire regeneration factors identified in this review, such as elevation and climatic stress variables, to identify post-fire locations that will have a high likelihood for natural regeneration success and where planting seedlings will have the highest chance for establishment and survival.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A Attributes of the 33 publications that we incorporated into our review of the factors driving ponderosa pine regeneration following wildfire.

Publication	Geographic state(s)	Number of wildfires	Publication type	Time(s) since wildfire
Bonnet et al. (2005)	SD	1	Journal article	2
Chambers et al. (2016)	CO	5	Journal article	11–18
Coop et al. (2019)	AZ, CO, NM, OR	12	Journal article	12–17
Davis et al. (2019)	AZ, CA, CO, ID, MT, NM	33	Journal article	8–24
Dodson and Root (2013)	OR	1	Journal article	10
Downing et al. (2019)	OR	4	Journal article	12–17
Foxx (1996)	NM	1	Conference proceedings article	1–16
Haffey et al. (2018)	AZ, NM	8	Journal article	7–17
Haire and McGarigal (2010)	AZ, NM	2	Journal article	32–49
Hankin et al. (2019)	ID, MT	18	Journal article	9–24
Kemp et al. (2016)	ID, MT	21	Journal article	5–13
Kemp et al. (2019)	ID, MT	21	Journal article	5–13
Keyser et al. (2008)	SD	1	Journal article	2–5
Lentile et al. (2005)	SD	1	Journal article	2–3
Lopez Ortiz et al. (2019)	CA	11	Journal article	18–19
Malone et al. (2018)	CO	1	Journal article	11–12
Ouzts et al. (2015)	AZ, NM	8	Journal article	8–13
Owen et al. (2017)	AZ	2	Journal article	12–13
Passovoy and Fulé (2006)	AZ	7	Journal article	3–27
Porter (2019)	CO	1	Thesis	15
Roccaforte et al. (2012)	AZ, NM	11	Journal article	1–18
Roccaforte et al. (2018)	AZ	1	Journal article	5
Rodman et al., 2019	CO, NM	15	Journal article	7–29
Rother and Veblen (2016)	CO	6	Journal article	8–23
Rother and Veblen (2017)	CO	5	Journal article	8–15
Savage et al. (2013)	NM	5	Journal article	52–64
Shive et al. (2013)	AZ	1	Journal article	8
Stevens et al. (2014)	CA	12	Journal article	2–5
Stevens-Rumann et al. (2012)	AZ, SD	2	Journal article	10
Stoddard et al. (2018)	AZ	1	Journal article	1–15
Strom and Fulé (2007)	AZ	1	Journal article	2
Wutke (2011)	SD	1	Thesis	10
Ziegler et al. (2017)	CO, SD	3	Journal article	11–15

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